

---

# PHYLOGENETIC ANALYSIS OF THE CICHORIOIDEAE (ASTERACEAE), WITH EMPHASIS ON THE MUTISIEAE<sup>1</sup>

*Per Ola Karis,<sup>2</sup> Mari Källersjö,<sup>2</sup> and  
Kåre Bremer<sup>3</sup>*

---

## ABSTRACT

We present a cladistic analysis of 53 taxa from Asteraceae using 72 characters of mainly morphological data. Results reveal subfamily Cichorioideae is paraphyletic. The Mutisieae constitute a basal grade that contains monophyletic groups with *Mutisia* and Cardueae sensu lato. The Arctotideae, Liabeae, Vernonieae, and Lactuceae form a clade together with subfamily Asteroideae. Our results show some inconsistencies with those from cladistic analyses of molecular data.

---

The relationships within the Asteraceae, discussed since Cassini and Lessing in the early nineteenth century, have been scrutinized using cladistic methods (Bremer, 1987; Jansen & Palmer, 1987, 1988; Jansen et al., 1990). Many results of cladistic analyses were inconsistent with the intrafamilial systems proposed by other authors (e.g., Carlquist, 1976; Cronquist, 1977, 1981; Jeffrey, 1978; Wagenitz, 1976). Jansen & Palmer (1987) demonstrated that Mutisieae–Barnadesiinae (Cabrera, 1961, 1977) form a sister group to the rest of the family, a finding that was corroborated by an apomorphic cpDNA inversion in the latter group. Bremer (1987) also came to this conclusion in his

cladistic analysis of the family, noting strong morphological support for this dichotomy. Bremer's (1987) analysis further supported the monophyly of the subfamily Asteroideae, and the subfamily Cichorioideae emerged as a paraphyletic assemblage. The analyses of Jansen et al. (1990) yielded quite different topologies. The only monophyletic groupings established in all trees, both Wagner and Dollo analyses, are the subfamily Asteroideae, the Vernonieae as the sister group to the Liabeae, and the Eupatorieae as a subclade within a paraphyletic Heliantheae sensu lato. Dollo analysis always supported a monophyletic Cichorioideae, but the Wagner analysis resulted in a paraphyletic Cichorioi-

---

<sup>1</sup> This study was supported by a grant for Compositae taxonomy and Asteraceae phylogeny from the Swedish Natural Science Research Council. We thank Arne Anderberg for discussions of complex cladistic analyses and for letting us examine material that he had on loan from K. We also thank one anonymous reviewer, Michael J. Donoghue, Vicki A. Funk, Larry Hufford, Christopher J. Humphries, Robert K. Jansen, Guy L. Nesom, Peter F. Stevens, and John L. Strother for valuable comments on earlier versions of the manuscript.

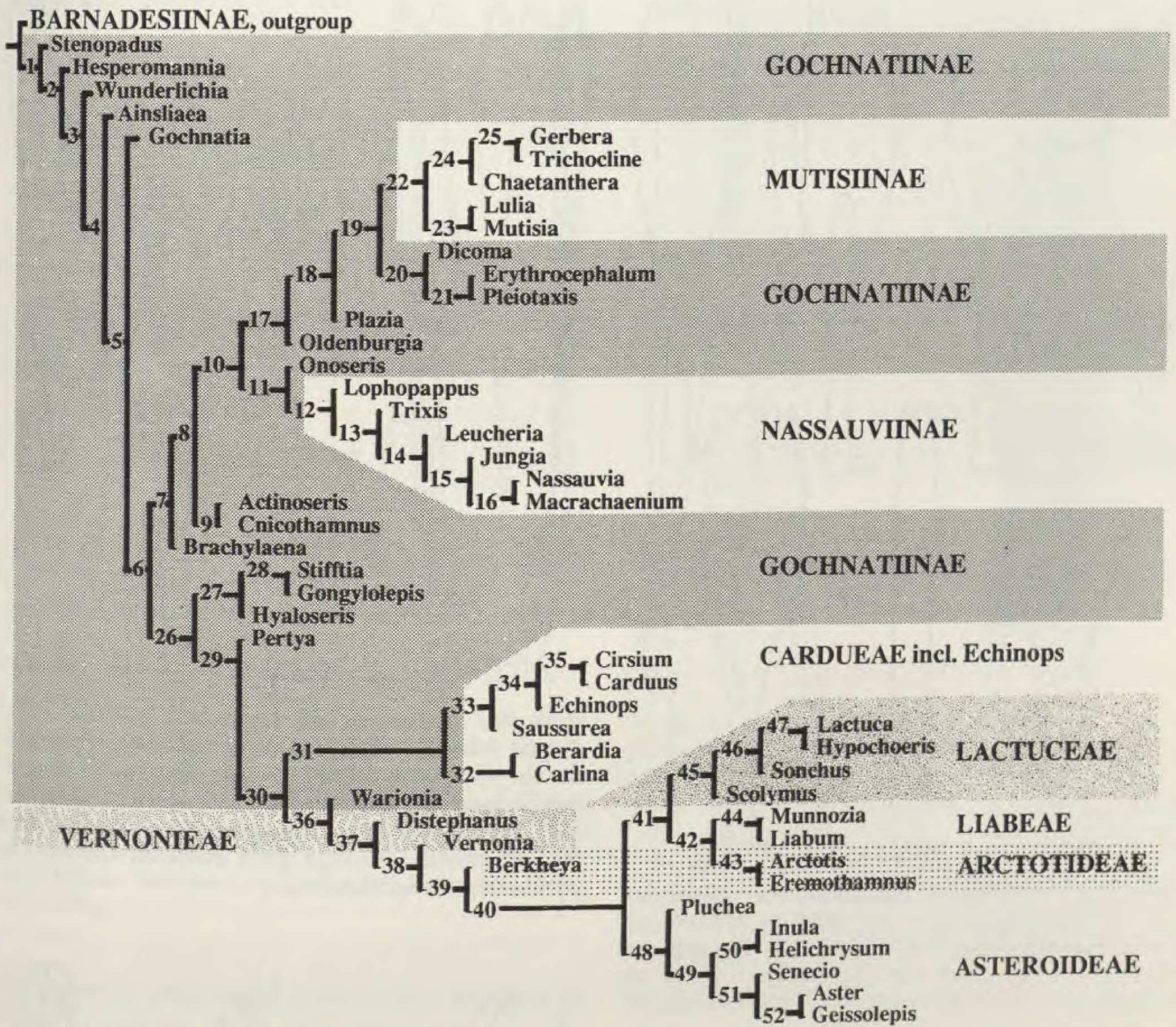
<sup>2</sup> Department of Phanerogamic Botany, Swedish Museum of Natural History, P.O. Box 50007, S-104 05 Stockholm, Sweden.

<sup>3</sup> Department of Systematic Botany, Uppsala University, P.O. Box 541, S-751 21 Uppsala, Sweden.

---

FIGURE 1. One of the two final cladograms. Character distributions are given below. Note that genera in the shaded area are all assigned to Mutisieae–Gochnatiinae. All apomorphies/reversals are listed for each node and each terminal taxon. Apomorphies with subsequent reversals/parallelisms are without further labeling, parallelisms are marked =, reversals are marked – with the change in multistate characters indicated within brackets. Multistate characters have the state in question indicated within parentheses. Under the terminal taxa all characters are parallelisms unless otherwise indicated.

Node 1: 28(0→1), 37, 65; =33(0→1); Node 2: 5, 58(0→1), 68; Node 3: 4, 30, 38(0→1), 42, 60; Node 4: 27(0→1), 29(0→1), 55; Node 5: –38(1→0); Node 6: 50, 51; Node 7: 15, =–42(1→0); Node 8: =16(0→1), =17, –29(1→0); Node 9: –4, –55; Node 10: =21, =48(0→3), =49(0→2); Node 11: –30; Node 12: =9, =16(1→2), =48(3→1), 59; Node 13: =1, =45, =46(0→2), =49(2→4), =58(1→3); Node 14: =66; Node 15: –15; Node 16: =29(0→1), =58(3→0); Node 17: –5, =23, =38(0→1); Node 18: –50, –55; Node 19: =1; Node 20: =5, =27(1→3), –28(1→0), =42(0→2), 64; Node 21: 8, =20; Node 22: =16(1→2); Node 23: =46(0→1), 48(3→4).



-58(1→0); Node 24: =18(0→1), -30; =58(1→3), -68; Node 25: =2(0→2), -60; Node 26: =21, =45, =46(0→1); Node 27: -5, -29(1→0); Node 28: -4, =12, -58(1→0), =69; Node 29: =38(0→1), =49(0→1), -68; Node 30: -28(1→0), =48(0→3); Node 31: =1, -60; Node 32: =19, -45, -46(1→0); Node 33: =20, =49(1→5), -55; Node 34: =3, =58(1→0); Node 35: 33(1→3), =39; Node 36: -4, -30, =42(1→2); Node 37: =32(0→1); Node 38: =1, 34, =68; Node 39: =15, =26, =29(1→2), 41, =48(3→2), =67; Node 40: 16(0→3); Node 41: -51, -55; Node 42: =4, =17, =18(0→1); Node 43: =32(1→2), -33(1→0), =48(2→3), -60, -68; Node 44: =24, -37; Node 45: =10, 13, -15, =16(3→4), 25(0→3), =32(1→2), 43, 54, =71(0→1); Node 46: =31, -33(1→0), =35, -58(1→0), -68, =70; Node 47: =55, 57; Node 48: =18(0→1), =19, -33(1→0), =48(2→1), 47(0→2), 72; Node 49: =36, 44, =49(1→4), -50; Node 50: -58(1→0), -60, =63; Node 51: =17, -37, -68; Node 52: =10, 28(1→2), =49(4→2), 53; Actinoseris: 1, 2(0→2), 25(0→1), 29(0→1), 45, 67, 69; Ainsliaea: 1, 18(0→1), -42(1→0), 66; Arctotis: 10, 19, -21, -26, 27(1→2), 28(0→1), -37, -38(1→0), 42(2→1), 49(1→5), 51, 52; Aster: -36, 50, 61; Berardia: 2(0→2), 20, -21, 26, 27(1→2), -58(1→0), 67, 71(0→1); Berkheya: 3, 4, 16(0→5), 18(0→2), 24, 28(0→1), 31; Brachylaena: 26, 27(1→3), -28(1→0), -68; Carduus: -4, -27(1→0), 42(1→2), -50, 52, 56, 62, 71(0→2); Carlina: 3, -4, 11, 14, 22, 23, 49(1→5), -50, 66, 71(0→2); Cirsiium: 36, 66, 67, 68; Chaetanthera: 10, 43(0→3); Cnicothamnus: -29(1→0), 36, 42(0→1); Dicoma: 18(0→1), 69; Distephanus: 29(1→2), -38(1→0), 48(3→1); Echinops: 24, -38(1→0), 52; Eremothamnus: -1, 3, 22, 29(2→1), 31, 35, -67; Erythrocephalum: 14, 29(0→1), 45, 46(0→1), 50, 58(1→2), 66, 67; Gerbera: 5, 29(0→1), 46(0→1), 50, 67; Gochnatia: 21; Gongylolepis: 6, 7, 16(0→2), 17, -46(1→0); Helichrysum: 4, -5, 11, 16(3→6), 46(1→2), 61; Hesperomannia: 32(0→1), 45, 48(0→1), 49(0→1); Hyaloseris: 10, 16(0→4), -30, -51, 58(1→2); Hypochoeris: 2(0→2), 14, -54, 66; Inula: 17, -21, 25(0→2), -32(1→0), 47(2→1), 48(1→3), 49(4→3), -67, 62; Jungia: 14, 32(0→1); Lactuca: 9, -25(3→0), 63; Leucheria: 25(0→2), 38(0→2); Liabum: 9, 22, -41, 55, 70; Lophopappus: 3, -5, -15, -50; Lulia: 18(1), 24, -37, -38(1→0), 39, 50, 61; Macrachaenium: 2(2), 32(1), 36, -46(2→1), -49(4→2); Munnozia: 27(2), 58(0), 71(1); Mutisia: -1, 25(1), 40, 45, -60, 66; Nassauvia: 3, -4, 38(2), -55, -66, 67, -68; Oldenburgia: 7; Onoseris: 18(1), 19, 24, 38(1), 39, 40, 42(1), 45, 62, -68; Pertya: 48(4), -50; Plazia: 22, 42(0→1), 45, 49(2→3); Pleiotaxis: 10, -15, -16(1→0), -17, -21, -23, 36, 49(2→3), 55, -68; Pluchea: -5, 16(3→6), 25(2), -32(1→0), -67; Saussurea: 56, 61, 70; Scolymus: 14, 24, 37, 67(2); Senecio: -5, 9, 38(1→2), 46(1→2); Sonchus: 3, 9, 24, 69; Stenopadus: 6, 7, 12, 22, 51, 55; Stiffia: 9, -42(1→0), -50, -68; Trichocline: -1, 39, 40, 48(3→4); Vernonia: -5, 22, -37, 66, 70; Warionia: 24, 27(1→3), 40, -50, -55, 62, 71(0→1); Wunderlichia: 22, 25(0→1).